CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society

Volume 35, No. 4 December 2006

XC .A104 v.35 #4

CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society
www.carnivorousplants.org

Volume 35, Number 4
December 2006

Front Cover: *Drosera intermedia* and *Drosera anglica* shown growing side by side at Vales Moor. Article on page 100. Photograph by Aidan Selwyn.

Back Cover: Two views of a young *Eucnide urens* plant. Article on page 119. Photograph by Michael Metzler.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Contributors should review the "Instructions to Authors" printed in the March issue of each year. Advertisers should contact the editors.Views expressed in this publication are those of the authors, not the editorial staff.

All correspondence regarding dues, address changes and missing issues should be sent to the Membership Coordinator at the ICPS. Do not send such correspondence to the editors. Checks for subscriptions and back issues should be made to the ICPS in US funds. Dues for 2006 are $25.

ICPS, Inc.
PMB 322
1564-A Fitzgerald Drive
Pinole, CA 94564-2229, USA
icps@carnivorousplants.org

JAN 17 2007
BOTANICA GARDEN

President	Carl Mazur, email: carl@carnivorousplants.org
Vice President	Cindy Slezak, email: cindy@carnivorousplants.org
Treasurer	Richard Myers, email: richard@carnivorousplants.org
Secretary, Seed Bank	John Brittnacher, email: john@carnivorousplants.org, seedbank listed in this issue.
Board Member	Chris Teichreb, email: chris@carnivorousplants.org
Board Member	Steve LaWarre, email: stevel@carnivorousplants.org

Editors:
Barry A. Rice, P.O. Box 72741, Davis, CA 95617, USA, email: barry@carnivorousplants.org
Jan Schlauer, Zwischenstr. 11, D-60594 Frankfurt, Germany, email: jan@carnivorousplants.org
Page Layout: Steve Baker, email: steve@carnivorousplants.org

Date of effective publication of the September 2006 issue of Carnivorous Plant Newsletter: 22 September 2006.

The ICPS is the International Cultivar Registration Authority (ICRA) for cultivated carnivorous plants according to The International Code For The Nomenclature of Cultivated Plants. Send relevant correspondence to the ICPS, Inc.

PUBLISHER: ICPS, Inc., Pinole, California. Published quarterly with one volume annually. Desktop Publishing: Steve Baker, 5612 Creek Point Drive, Hickory, NC 28601. Printer: Kandid Litho. Logo and masthead art: Paul Milauskas. Dues: $25.00 annually. © 2006 Carnivorous Plant Newsletter. All rights reserved. ISSN #0190-9215.

Contents

Seedbank ----- 99
Carnivorous Plants in the New Forest ----- 100
The time memory of the Venus flytrap (*Dionaea muscipula* Ellis) ----- 108
Insecticidal Characteristics of the Desert Stingbush *Eucnide urens* ----- 119
Looking Back: CPN 25 years ago ----- 121
Additional notes on *Eucnide urens* (Parry ex Gray) Parry in the Family Loasaceae ----- 122
News and Views ----- 124
Index of Contributors ----- 127

International Carnivorous Plant Society Seed bank
ICPS Seedbank• P.O. Box 71 • Ashland, OR 97520-0003 • USA

Dionaea muscipula
Drosera aliciae
D. anglica
D. auriculata
D. binata
D. binata—Coromandel, NZ
D. burmannii
D. capensis 'Albino'—white flower
D. capensis—narrow leaf
D. capensis—red leaf
D. dielsiana
D. filiformis var. *filiformis*
D. filiformis var. *tracyi*
D. glanduligera
D. intermedia—Cuba
D. intermedia—New Jersey, USA
D. intermedia—North Carolina, USA
D. intermedia—Rhode Island, USA
D. intermedia—Venezuela
D. macrantha subsp. *macrantha*
D. peltata
D. rotundifolia—Alaska, USA
D. rotundifolia—Newfoundland, Canada
D. rotundifolia—Washington, USA
D. stolonifera subsp. *porrecta*
D. tokaiensis
Pinguicula alpina
Sarracenia alata—Texas, USA
S. flava
S. leucophylla
S. purpurea subsp. *purpurea*
S. purpurea subsp. *venosa*
S. rubra subsp. *jonesii*—ESA/CITES, USA sales only
S.—various hybrids

PLEASE NOTE the new address for the ICPS Seedbank!

This is a partial list of the seeds available. A complete list is online at the ICPS web site, http://www.carnivorousplants.org/ or by sending a self-addressed, stamped (if USA), envelope to the seed bank address.

Seed packets are US$1 each. Please include US$3 postage and handling for each order. You may pay by cash, check, or money order in US$. Many members pay with cash. Please make checks and money orders payable to "ICPS Seed Bank".

The seed bank is a members-only benefit. The quantity of seed available to each member is 1 packet of each variety per month and 40 packets total in any 12 month period. Please list alternative seed selections, as other orders will arrive before yours. If you have an e-mail address, please include it so we can correspond should any issues arise. Seeds purchased through the seed bank are intended for your personal use only and may not be sold.

You are encouraged to stock the seed bank with seed produced by cultivated plants. The ICPS policy on wild seed collection is on line at the ICPS web site. Cultivation-produced seeds of species protected by the US Endangered Species Act are distributed within the US only, and in accordance with the ICPS's US Fish &Wildlife Service permit TE061005-1.

Donate seed and get credit for free seed from the seed bank. Seeds of selected varieties are available free to teachers for use in the classroom and to scientists and conservation organizations. It is ICPS policy not to sell internationally seed of plants protected by CITES Appendix I or the US Endangered Species Act.

John Brittnacher, Manager • john@carnivorousplants.org

Carnivorous Plants in the New Forest

Stephen Locke • Aidan Selwyn • 7 Complins• Holybourne• Alton • Hampshire • GU34 4EH • United Kingdoms • aidanselwyn@jktree.fsworld.co.uk

Keywords: travelogue: Great Britain, *Dionaea*, *Drosera*, *Pinguicula*, *Utricularia*.

Introduction

The New Forest is a 37907 ha area of outstanding ecological and natural history interest in central southern England, and a prime area for native carnivorous plants. Its biodiversity and ecology are recognized and protected under a range of British and European measures. Much of this importance is due to the preservation of formerly widespread ancient habitats, some of which can be traced back to prehistoric times, which have been lost elsewhere. Its value as a refuge for flourishing populations of carnivorous plants is part of, but completely dependent on, the overall ecological importance of the area. This summary of the New Forest is largely derived from the works of Colin R. Tubbs (1986, 2001), the most recent and authoritative accounts of the history, ecology and conservation of the New Forest. Anybody seriously interested in the New Forest should refer to these two books. This paper is restricted to a treatment of the carnivorous flora of the New Forest.

The New Forest is not an unbroken woodland. It is a series of eroded flat terraces, highest in the north (120-128 metres altitude), lowest in the south. The middle terraces are scoured into wide hollows drained by two south-flowing stream systems which reach the sea at the Solent (the straights between the Isle of Wight and the mainland). The terrace surfaces are mostly mantled in heathland, and the hollows and valleys between them are a mosaic of woodland, heath, grassland and mire. Superimposed are the mainly regular blocks of woodland (chiefly planted under specific Acts of Parliament) and the more rounded blocks of farmland and settlements.

The New Forest is anything but new to us, but it was new to William I who formed it sometime between the Norman Conquest (1066) and 1086. The history of the New Forest as a legal and administrative entity is long and extremely complex, and arguably this very complexity, and the existence of many parties with rights, obligations or influence has contributed to the survival of its unique character: no one authority has, over a long enough period of time, completely dominated the Forest and its management so as to constrain it to a single purpose. During the 20th century, controversy over the role of commercial forestry came to a head and in 1970 the Minister for Agriculture imposed a temporary ban on felling broadleaved trees, thus establishing the primacy of ecological conservation that is now the basis for environmental planning of the Forest. The New Forest was recently designated as a National Park.

The New Forest is an ecological system which is constantly developing under the influence of large, free-ranging herbivores; both domestic stock and deer. It is the largest area of wild, unsown vegetation in lowland Britain, and includes the largest remaining tracts of intact heathland (12,500 ha), valley mire (2900 ha), and ancient pasture woodland. These three habitats were formerly common, but are now fragmented and rare in lowland Western Europe. As such the New Forest is of global importance. The mire and wet heath habitats are the most interesting to carnivorous plant enthusiasts, but it is essential to emphasise the relationship between all the diverse mosaic of habitats upon which the biological health and diversity of the New Forest depends. The impact of large herbivores over centuries, indeed millennia, is a particularly critical factor.

Finally, we should emphasise the fact that many people live in the New Forest and very many more visit it. There are numerous settlements in the Forest and it is situated in the heart of densely populated central southern England with the urban areas of Bournemouth and Southampton crowding in from the west and east respectively. It is a place of recreation for mil-

Figure 1: *Dionaea muscipula* at Vales Moor. Photograph by Aidan Selwyn.

Figure 2: *Pinguicula lusitanica* at Vales moor. Photograph at lower right by Stephen Locke, others by Aidan Selwyn.

lions of people: about 15 million live within 1 1/2 hrs drive of the Forest. Users of the Forest range from those relatively few who depend on it for their actual livelihood, to casual visitors who stay close to the roads and treat it essentially as a park, to the dedicated walkers and naturalists who penetrate deeper into the forest, among whom we can include carnivorous plant enthusiasts. These hikers come in no small numbers, and carry with them the potential to significantly disturb sensitive wildlife areas.

Carnivorous Plants in the New Forest

As in many parts of the world, the distribution of carnivorous plants in Britain has been severely reduced, for the common reasons of drainage of wetlands, agricultural intensification and urban development. It is instructive to compare historic records of carnivorous plants in the New Forest with their current distribution, and occurrence elsewhere in Hampshire. The major sources for records are the 2 primary Hampshire county floras (Townsend 1904; Brewis *et al.* 1996) and the Hampshire County Museum Service herbarium. It is clear that the current distribution of carnivorous plants in the New Forest is broadly similar to the historic records. This is in strong contrast to the losses elsewhere in Hampshire and indeed Britain as a whole, and doubtless reflects the greater degree of protection afforded the New Forest and above all the lack of agricultural intensification.

Drosera

Drosera rotundifolia and *D. intermedia* are recorded in both floras as very generally distributed and common in the New Forest, as they are today. Likewise, both floras record *D. anglica*, but state it to be rare.

Brewis *et al.* (1996) record *D.* × *obovata* (*D. anglica* × *D. rotundifolia*) as very rare. Townsend (1904) does not record *D.* × *obovata*. Specific localities given for all these species correlate with where they may be found now and herbarium specimens confirm this.

Pinguicula

Pinguicula lusitanica is said by Townsend (1904) to be characteristic of turfy bogs and at that time frequent in the New Forest. Brewis *et al.* (1996) state that *P. lusitanica* is frequent and often plentiful in the New Forest, but very rare elsewhere in Hampshire. Neither flora records *P. vulgaris* from the New Forest. Again, the herbarium confirms this picture. There are however persistent rumours that *P. vulgaris* does occur, either wild or planted.

Utricularia

The distribution of *Utricularia* is confused by the problems of taxonomy and identification. Taylor (1989) was unable to resolve a number of taxonomic issues relevant to the species in the New Forest, so it is clearly beyond the competence of the present authors! Townsend (1904) records *U. vulgaris* L; *U. neglecta* Lehm.; *U. intermedia* Hayne; and *U. minor* L from the New Forest. Brewis *et al.* (1996) record only two *Utricularia* species for the New Forest: *U. intermedia* from a small number of locations, and *U. minor* as locally frequent (especially in the south). They consider records of other species to be misidentifications. The herbarium records conform to this with the proviso about the difficulties of identification. The overall picture that emerges is that only *U. intermedia* and *U. minor* are certainly recorded from the New Forest, and that *U. minor* is the more common and widespread species.

One of the issues not resolved by Taylor (1989) is the status of *U. ochroleuca* R Hartman. The species *U. ochroleuca* and *U. intermedia* are difficult to distinguish (at least as far as historic records are concerned). Neither of the floras or the Hampshire herbarium use the taxon name *U. ochroleuca*, but the presence of this species—under the name "*U. intermedia*"—cannot be ruled out. In summary, the distribution of *Utricularia* seems to have been broadly maintained but

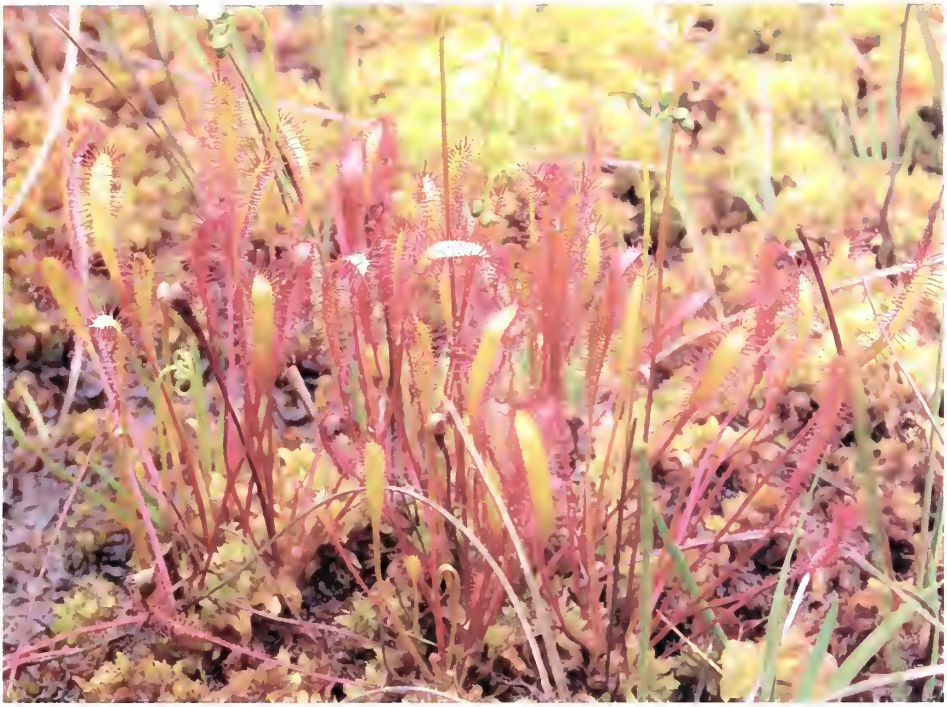


Figure 3: *Drosera anglica* at Vales Moor. Photograph by Aidan Selwyn.

Figure 4: *Drosera* × *obovata* at Vales Moor. Photograph by Aidan Selwyn.

problems of identification make detailed comparisons between species difficult. Certainly two species of *Utricularia* occur, conventionally identified as *U. intermedia* and *U. minor*, and *U. minor* seems to be the more widespread; although its greater propensity to flower makes it more noticeable. It would be useful to obtain some authoritative determinations of material from the New Forest to clarify the current distribution.

Sarracenia and *Dionaea*

Brewis *et al.* (1996) note that *Sarracenia flava* was apparently planted in a valley bog in the New Forest near Burley as early as 1903, and this planting was subsequently observed in 1983, 1987 and 1992. However, they do not record *Dionaea muscipula*, which has also been planted in the New Forest and is still surviving in at least one locality at the time of writing.

Viewing carnivorous plants in the New Forest

The following account of a day spent visiting just three sites in the New Forest demonstrates the relative ease with which its carnivorous plants may be seen in an area of outstanding natural history.

In the last week of July, the authors, accompanied by Nina Locke and Susan Walkinshaw, visited three bogs within the New Forest. Stephen has visited the area over a number of years and acted as our guide. After a month of dry weather there had been almost continuous rain over the 48 hrs preceding our visit. That day, conditions proved to be cool, dry, overcast and breezy. This made photographing small subjects something of a challenge and Aidan, who has contributed most of the illustrations in this article, shot 171 frames in the hope of capturing some acceptable images.

The first location was Vales Moor, and the road passes through the bog itself. Parking the car on the verge, we were confronted by masses of sundews as soon as we stepped into the bog. Both *D. intermedia* and *D. rotundifolia* were growing in profusion. The bog is substantial and we spent some time quartering the area looking for a particular plant that we knew to have been present in previous years. At this point, Aidan had his first face-to-face encounter with the UK's only venomous snake, the adder (*Vipera berus*) which he located by the simple method of very nearly stepping on it! It was brown, which indicates that it was probably female; it quickly moved off into the undergrowth.

We had almost given up searching when Nina spotted a flower scape emerging from the surrounding grasses. She had found what we were all looking for: *Dionaea muscipula* growing wild in the south of England! Two apparently healthy adult plants nestling amidst a patch of *Sphagnum*, busily catching prey. One plant had flowers that were soon to open, the other had an aborted scape (see Figure 1). There was no evidence of the plants dividing or of any seedlings nearby and they were clearly under intense competition from the native vegetation. There are said to be a number of sites in the forest where *D. muscipula* has been introduced, and while Stephen had seen them before this was the first time Aidan had actually seen the plant growing wild. Shortly thereafter, Stephen found the finely veined rosettes and pink flowers of the diminutive *P. lusitanica,* growing in an area of exposed peaty substrate. This is a minute plant that is easily overlooked and difficult to photograph on a windy day (see Figure 2).

Crossing the road and entering the other side of the bog revealed yet more sundews, including the largest species, *D. anglica* (see Figure 3) and the similarly sized hybrid *D.* × *obovata* (see Figure 4). *Drosera anglica* and *D. intermedia* are often mistaken for one another, but seen growing in the same location, the differences between the two plants are obvious. *Drosera anglica* is by far the larger plant in all respects (see Front Cover).

Having seen all of our native *Drosera* species in a single bog, we moved on to the second location, Holmsley Bog, which is a limited area of bog in the bottom of a small river valley. Sundews were evident, but we saw no further carnivorous plants of interest, although Stephen had noted *Utricularia* on previous visits. The bog was however home to an interesting funnel-weaver spider (*Agelena labyrinthica*) spotted by Aidan, living in the centre of a large funnel-web.

Figure 5: Wootton Bog general view, featuring Aidan Selwyn and Susan Walkinshaw way off in the distance. Photograph by Stephen Locke.

Figure 6: Very large *Drosera rotundifolia* growing submerged at Wootton Bog. Photograph by Aidan Selwyn.

Figure 7: *Utricularia minor* at Wootton Bog. Photograph by Aidan Selwyn.

Figure 8: Stephen Locke photographing plants at Wootton Bog. Photograph by Aidan Selwyn.

Aidan spent some time attempting to photograph the creature and its prey item.

We drove to our final location, Wootton Bog. It proved to be a very wet bog (see Figure 5). The ground was saturated with areas of open water and it was difficult to find firm footing that would support our weight. *Drosera intermedia* and *D. rotundifolia* were again present in large numbers and we found what was perhaps the largest example of *D. rotundifolia* that we had seen (see Figure 6). Growing almost entirely submerged, the leaf rosette was 10-12cm in diameter. Susan made our final find of the day: the tiny and bright yellow flowers of *U. minor* on their scapes rising from pools of water (see Figure 7).

A very enjoyable day in good company, our field-trip in the forest was a notable success and we could not have hoped to see a greater variety of plants. The one carnivorous plant native to the forest that we did not see was *U. intermedia*. Unless in flower, *Utricularia* are not easy to find at the best of times and we were fortunate to locate *U. minor*. Even a relaxed excursion such as ours demonstrated the quality and diversity of carnivorous plant habitats in the New Forest. It has certainly served to maintain our interest in the area and we are resolved to make a rather more intensive search for *Utricularia* next year!

Acknowledgement: We are grateful for the assistance of Hampshire County Council Museums and Archives Service for access to their herbarium

References:

Brewis, A., Bowman, P., and Rose, F. 1996. The Flora of Hampshire. Harley Books.

Townsend, F. 1904. Flora of Hampshire including the Isle of Wight. Privately published.

Taylor, P. 1989. The genus *Utricularia* - a taxonomic monograph. Royal Botanical Gardens, Kew, United Kingdom.

Tubbs, C.R. 2001. The New Forest: History, Ecology & Conservation. New Forest Ninth Centenary Trust.

Tubbs, C.R. 1986. The New Forest. Collins.

The time memory of the Venus flytrap (*Dionaea muscipula* Ellis)

Arne Molis • Gabriele Patten • Manfred Weidner • Universität Köln • Botanisches Institut • Gyrhofsstrasse 15 • 50923 Köln • Germany •manfred.weidner@uni-koeln.de

Keywords: physiology: *Dionaea muscipula.*

Summary

For closure to occur, the trap leaves of the carnivorous Venus flytrap (*Dionaea muscipula* Ellis) normally must be stimulated twice. This is achieved by touching the bending-sensitive hairs protruding from the upper leaf surface. This triggers a rapid thigmonastic capture movement of the leaf lobes. This way incidental closure movements are avoided. The maximal memory time, i.e. the time limit between the first and the second stimulation event, which must not be exceeded, is highly variable and ranges between 20—80 s. Our investigation explores the influences of external (environmental) and internal (plant specific) factors on this memory time. Throughout in this study, a "50%-closure-value" was determined for each variable on basis of 50—100 independent measurements. The memory effect exhibits inverse and sigmoidal temperature characteristics, thus showing a maximum memory time at lower temperatures (15°C). Moreover, the daily photon fluency, the age of the trap leaves, seasonality (the time of leaf emergence), and the recovery time between consecutive stimulation cycles, all affect the time memory strongly. Further, the topology of stimulation also exerts a large influence: The time memory fades more rapidly when two different trigger hairs were stimulated successively within the time limits of the memory instead of touching the same hair twice.

Introduction

The evocation of trap leaf closure in the Venus flytrap, *D. muscipula* Ellis, is a unique phenomenon in nature, because this movement normally occurs only after two successive mechanical stimulations of the 3 (-5) special hairs. These 3 to 5 trigger hairs, acting as mechano-sensors, are protruding from the abaxial surface of the two trap lobes (Haberlandt 1906; Guttenberg von 1925; Williams and Mozinga 1971; Juniper *et al.* 1989).This unparalleled behaviour was characterised as manifestation of a "time memory" (Brown & Sharp 1910; Jacobson 1965). We adopt this term but do not intend to imply any explanation for the mechanisms underlying the phenomenon. Evidently, the information of an initial stimulation event is "stored" for a period of about one minute. During this time-span, the leaf is in a preconditioned state for subsequent closure and thus susceptible to a second stimulation; it closes extremely fast upon re-stimulation. Occasionally, more than two stimulations may be required, or closure may be triggered by just one triggering event (Brown 1916; Jacobson 1965; Sibaoka 1966; Williams 1973; Hodick & Sievers 1986, 1988, 1989; Trebacz 1996). However, no systematic and comprehensive description of the phenomenon has ever been undertaken. It was our intention to lessen this gap and evaluate some prominent phenological aspects of the time memory of *D. muscipula*, striving for elucidation of the influence of external as well as internal factors.

A highly condensed recapitulation of the present stage of our knowledge on trap leaf closure with special regard to the time memory of *D. muscipula* is helpful to understand the experimental facts presented and discussed below. Ion fluxes, involving Ca^{2+}, K^+ and Cl^-, cause rapid changes of the cell membrane potential of leaf parenchyma cells, and thus are responsible for the triggering of trap closure. Depending on stimulus-strength, the mechanical stimulation is transduced into a receptor potential, generated in specialised mechano-sensitive cells at the base of a trigger hair (Haberlandt 1906; Benolken & Jacobson 1970; Williams & Mozingo 1971; Casser *et al.* 1985; Hodick & Sievers 1988). If the excitation is strong enough, the receptor potential triggers an action potential ("AP"), which—as a circular depolarisation wave of the cell membrane potential—spreads rapidly across the lobes of the trap leaf (Burden-Sanderson & Page 1876; Williams & Pickard 1980; Hodick & Sievers 1986, 1988; Sibaoka 1966, 1991; Trebacz *et al.* 1996; Volkov *et al.* 2002). Upon arrival of a second AP—evoked within the limits of the memory time—epidermal

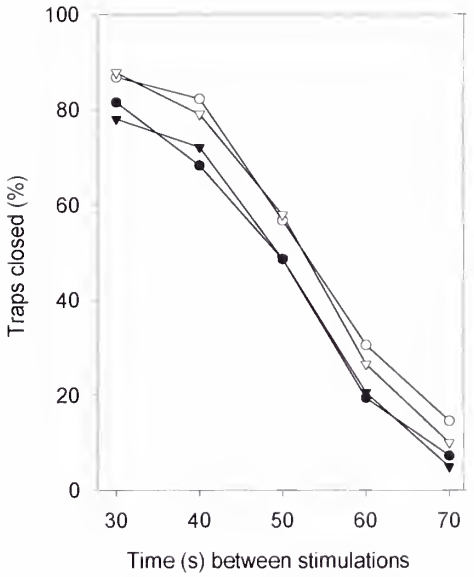


Figure 1: Comparison of traps responding to two stimulations with complete closures (data shown with open circles and open triangles), and traps that responded with either complete or partial closure (i.e. "all closures"; data shown with filled circles and filled triangles). Two series of measurements were executed, one is indicated with circles, the other with triangles.

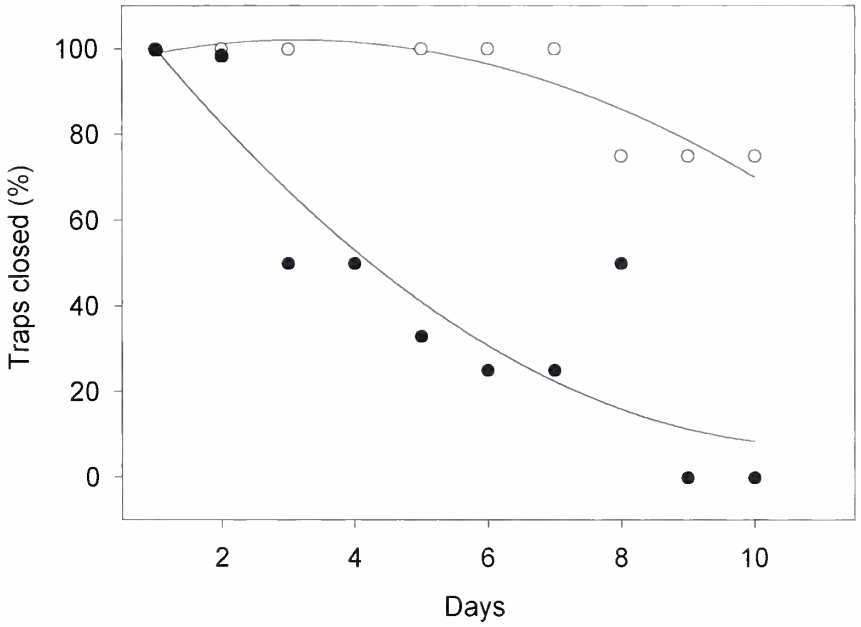


Figure 2: Stimulation repetition experiment: Relatively young trap leaves (3 weeks after emergence) were subjected to 10 stimulation/closure/re-opening cycles. The time lapse between cycles was 24 hours. The interval between first and second stimulation was set at 20 s, which ensured 100% closure at the beginning of the experiment (cycle 1). Complete closures (filled circles) and all closures (open circles) were compared.

and mesophyll cells which are anatomically and physiologically equipped to undergo small changes in cell shape (Guttenberg 1926; Benolken & Jacobson 1970; Haddock & Sievers 1989; Juniper *et al.* 1989) initiate the extremely rapid closure movement of the trap leaf by means of a "snap-buckle" mechanism, as revealed only recently by Fortiori *et al.* (2005).

A breakthrough of equal rank in understanding the second enigmatic feature of *D. muscipula* besides the extreme velocity of movement, the time memory, has not occurred yet. It has been suggested that an abrupt increase of the cytosolic Ca^{2+}-concentration ("$[Ca^{2+}]_{cyt}$"), brought about by stretch-activated Ca^{2+} influx-channels located in the plasmalemma, does not only evoke the generation of receptor potentials and of subsequent APs, (Cosgrove & Hedrich 1991; Wayne 1994; Malone 1996; Trebacz *et al.* 1996), but is as well decisive for the establishment of the time memory. A critical $[Ca^{2+}]_{cyt}$ threshold concentration must be attained or surpassed in epidermal and mesophyll cells engaged in trap closure in order to trigger the closure movement (Hodick & Sievers 1986, 1988; Trebacz *et al.* 1996). Assumedly, this critical level is reached only after the generation of a second AP, which causes a second Ca^{2+} influx-wave, superimposing the first one which not yet has levelled off. Possibly this occurs through the activation of plasma membrane depolarisation-activated Ca^{2+} channels (DACCs) by the APs. ATP-fuelled Ca^{2+}-pumps are thought to counteract this induced increase in $[Ca^{2+}]_{cyt}$ by continuously shuffling calcium from the cytosol back into the calcium storage pools, i.e. into the apoplast, and probably also into the cisternae of the endoplasmatic reticulum (ER) of the cell (Harper 2001; Hetherington & Brownlee 2004). If the second threshold-breaking AP is not generated in time, the $[Ca^{2+}]_{cyt}$ declines to a level too low for the second Ca^{2+}-inburst to push $[Ca^{2+}]_{cyt}$ beyond the threshold. In this case, the memory time is exceeded and trap closure does not occur.

Our new data on the influences of internal and external factors on the time memory of *D. muscipula* should be useful when the cell biological and molecular aspects of the time memory—in part still highly hypothetical—are reconsidered. Moreover, any future investigations may take advantage of the design and standardization of the experiments in our study.

Materials and Methods

Flytrap plants (*Dionaea muscipula* Ellis) were obtained in May 2001 from "Gartenbau Weilbrenner", 67251 Freinsheim (Germany). The potted plants (8 cm diam.) were grown in plastic trays containing 1-2 cm of natural rain water, free of HCO_3^-. They were cultivated in a greenhouse under natural light. The plants were initially sprayed with Bulldock® (Bayer AG, Germany) insecticide, and subsequently protected from *Sciaridae* re-infestation by screen enclosures and sticky yellow pads (Gelbtafeln). These precautions minimised undesirable closing of the trap leaves.

All experiments were executed between mid-May and August 2001. Thereafter, senescence of the trap-leaves (as well as flowering) became a problem. It seemed important from the beginning to be aware of the seasonality of trap-leaf development (Roberts & Oosting 1958). Therefore, date of emergence and morphometric leaf parameters that were suspected to exhibit seasonal differences (i.e. trap size and shape, petiole-length, and leaf colour) were carefully recorded for each plant, because they could possibly influence the time memory. The leaves of all the plants were marked and catalogued with a thin, water-resistant marker pen within one week after appearance, so a detailed time record was established enabling us to select uniform plants and trap leaves for each experiment.

Several days before the experiments were started, the plants chosen were transferred into a growth chamber; conditions were: 25°C, RH 60%, and continuous fluorescent white light (Osram L 58W/25; photon fluency density 110-150 µmol m^{-2} s^{-1}) 24 hours a day. Once again, sticky yellow pads were employed to capture flying insects. Each trap leaf was used for up to three thigmonastic experiments, allowing for a two-day recovery period between experiments. Thereafter the plants were brought back to the greenhouse for at least two weeks before they became candidates for another series of measurements.

Uniform batches of 10 and 30 *D. muscipula* plants, chosen by visual inspection, were included in one experiment, selecting 2-3 trap leaves from each plant. Thus, one set of data, i.e. one statistical mean, was made from at least 30 individual measurements. All recordings of the time memory were taken between 9 and 12. a.m.

The trigger hairs were stimulated by hand with the tip of a paper clip. Unless stated otherwise, the same trigger hair was used for the first and the second stimulation. The second triggering was

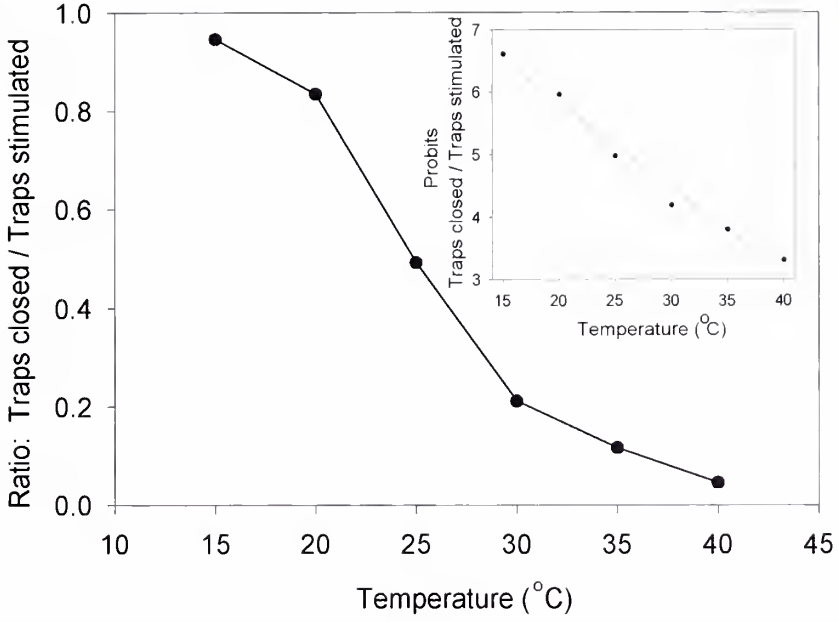


Figure 3: Temperature curve of the time memory of *D. muscipula*. The sigmoidal time memory decreases with rising temperature. The time interval between first and second stimulations was set at 60 s; under these conditions, the traps showed 50% closure at 25°C. The insert shows a Probit transformation of the above data.

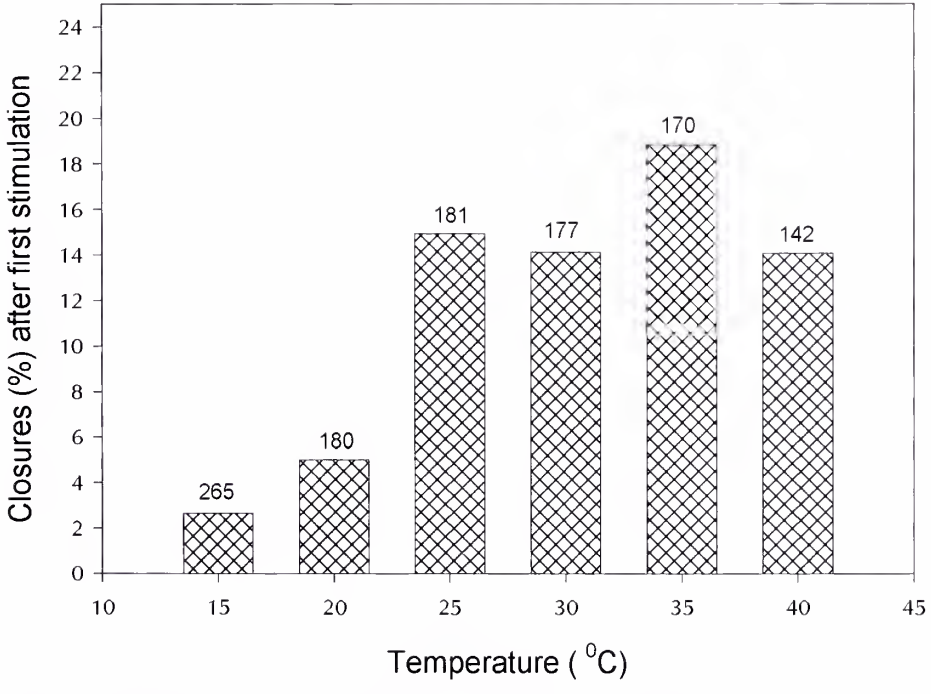


Figure 4: Percentage of closures induced after only one stimulation as a function of temperature. Included are the numbers of traps investigated at each temperature.

executed at variable times after the first one, depending on the particular experimental design. The response of the trap leaf was recorded as either "no closure", "complete closure" (tooth edges of the leaf lobes interlocking), or "incomplete closure" (which includes all responses short of total closure). By merging the values for "complete closures" and "incomplete closures" the category "all closures" was obtained. The time memory was determined by varying the time-lapse between the two consecutive stimulations in the range of 10—80 s in steps of 5—10 s. The percentage of responding traps, expressed either as "complete closures" or "all closures" were fitted into a curve with the time-lapse between stimulations plotted on the abscissa. This way, a curve was obtained that displayed a dose-effect for the memory time. From these plots, the time interval between stimulations for the 50% response was interpolated. This parameter was taken as our quantification of the memory-effect and as such was the basis for characterizing the effects of the external and internal factors on the time memory. In some experiments, e.g. the temperature curve, only one pre-tested time interval was employed.

Incomplete and Complete Trap Closure

It is important to define what is meant by a closure response by the trap. Is it important in our study that a trap leaf responds with complete closure, where the leaf margins tightly interlock or should all touch-induced trap movements, including the incomplete ones, be rated as positive responses?

We compared the time memory of trap stimulations that resulted in complete closures with the time memory of all trap stimulations that resulted in closure (both complete and incomplete). We observed only a moderate difference in the time memory between the two modes of recording (see Figure 1); both, shape and slope of the two response curves were identical. Therefore we conclude that it is insignificant whether the time memory data are compared on the basis of all closures or only complete closures. We used data from all closures in most cases, assuming that the partial closing of a trap leaf cannot be attributed in a causal way to the time memory mechanism itself. In fact, the decidedly parallel course of the two curves suggests that trigger hair stimulation and signal transduction on one side and the mechanical aspect of the closure movement of individual traps on the other side are separate elements of the closure mechanism as a whole. Evidently, only the latter aspect is affected when incomplete closure takes place.

The next experiment takes advantage of the ability of *D. muscipula* trap leaves to reopen repeatedly after an unsuccessful capture movements (Stuhlmann 1948; Jaffe 1973). A trap leaf can be stimulated to close up to 10 or more times, if a recovery time of 24 hours between stimulations was provided. However, upon such repeated stimuli, the percentage of stimuli that resulted in complete closure decreased rapidly (see Figure 2). By the fifth stimulation cycle, only 50% of the traps responded with a complete closure. After 9 repetitions, complete closures no longer occurred. Since the number of times a trap was previously stimulated to close does not affect the trap's time memory, but does modify how the trap is likely to close, this strengthens the view that the time memory and the closure process *in sensu strictu* are distinctly separate aspects of the trap leaf movement. Furthermore, it indicates that each closure movement negatively and quite enduringly affects the physiological state of the trap leaf engaged in the closure process. In other words, the cells and tissues engaged in the closure mechanism are more sensitive—in a metabolic and energetic sense—to optimal conditions than the cells and tissues involved in the time memory. The rapid decline of the ability of the trap to respond with complete closure suggests that those critical cell physiological conditions were not fully re-established, even though the re-opening movement of the incompletely closed traps was unhampered.

Influence of Temperature on the Time Memory

The first environmental factor to be investigated was temperature. In this test, the second stimulation of the trap leaves was executed 60 s after the first one. This setting was found appropriate for the trap leaves chosen for this experiment. At each temperature ≥ 60 traps were tested. The resulting curve exhibits a markedly inverse relationship (see Figure 3) between temperature and memory time. When temperature was increased from 20 to 30°C, the percentage of closures dropped from 84% to 21%, which corresponds to a Q_{10}-value of about 4 for the medium temperature range. The negative correlation suggests that the pronounced prolongation of the memory time,

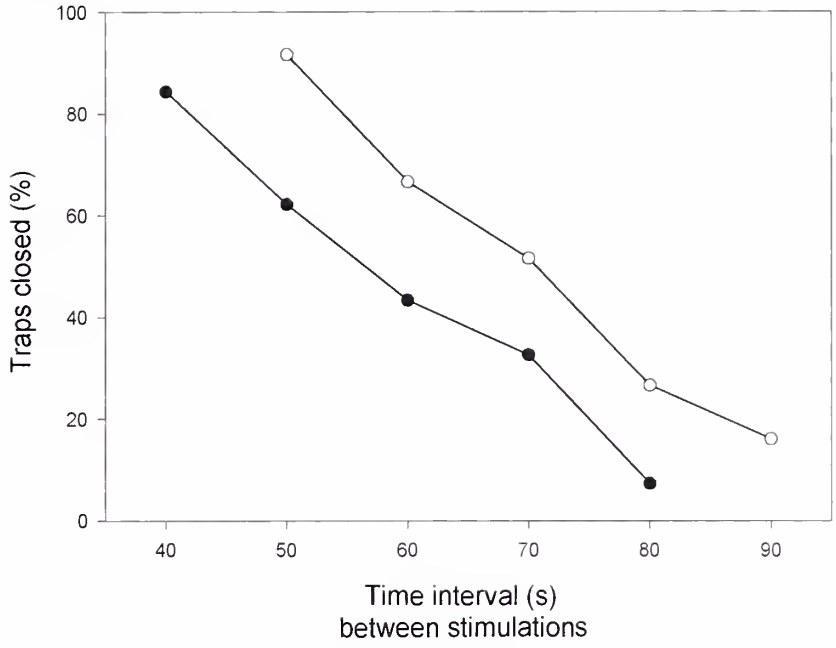


Figure 5: Influence of the daily light period on the time memory. Short-day conditions (8 hours light/16 hours darkness; filled circles) and continuous irradiation (24 hours light/0 hours darkness; open circles) were compared.

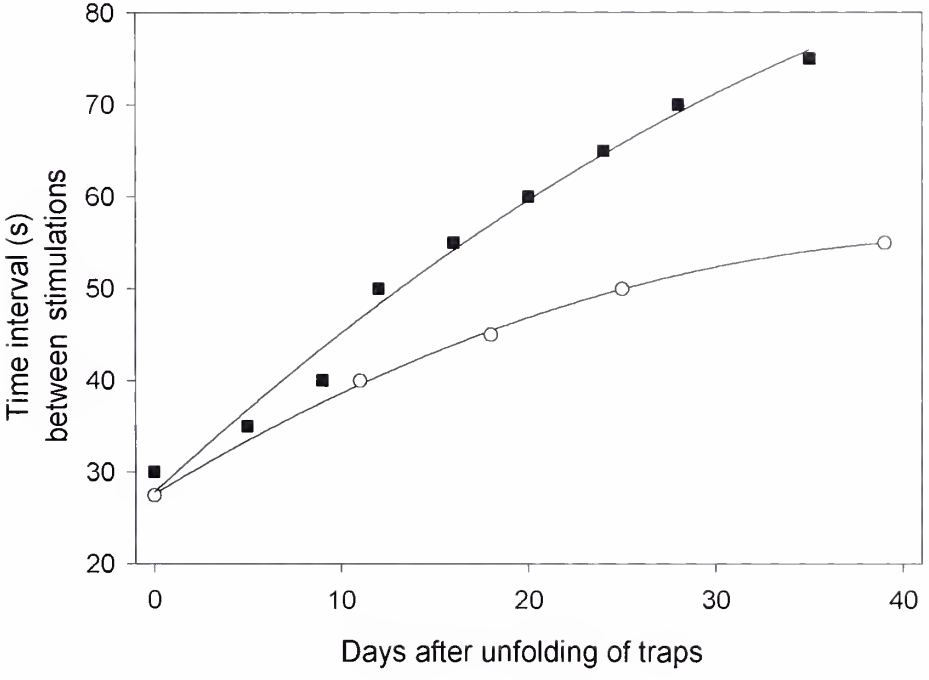


Figure 6: Seasonal shift of the time memory: All age-classes of trap leaves show higher values in mid-May (filled squares) than in late June (open circles).

observed at lower temperatures, may be attributed to the slow-down with falling temperature of an as yet unknown biochemical or biophysical process, which somehow interferes with the memory-sustaining physiological process. In addition, the temperature curve for the time memory of *D. muscipula* is sigmoidal, as confirmed by a Probit-transformation of the data (see Figure 3, Insert). Near the lower and the upper ends of the temperature curve, changes in time memory were much smaller. Beyond 30°C, practically none of the leaves closed after the 60 s time interval between first and second stimulus.

Sometimes, trap leaves close after only one stimulation of a trigger hair (Brown & Sharp 1910; Sibaoka 1966). We examined possible influences of temperature on this phenomenon. While about 14% of the traps responded after only one triggering at 25°C, the percentage declined to about 3% at 15°C (see Figure 4). This result suggests that the proposed $[Ca^{2+}]_{cyt}$ threshold value is especially low in such hypersensitive traps, and is therefore exceeded without a second Ca^{2+}-influx wave being initiated. Following this line of reasoning, one may conclude that the stimulation-induced increase in $[Ca^{2+}]_{cyt}$, has a markedly positive temperature coefficient. Alternatively, it may be imagined that the depolarisation amplitude of the first AP, and thus the resulting initial rise in $[Ca^{2+}]_{cyt}$, is outstandingly high in such trap leaves and consequently a second push of $[Ca^{2+}]_{cyt}$ is superfluous.

Effect of the Duration of Daily Irradiance

A significant difference in the time memory is attained when the daily photon fluency (mmol quanta m^{-2}) was changed. In addition to our standard setting—continuous irradiation—we included short day conditions, simulated by 8 hours of illumination and 16 hours of darkness. We apologize for not also investigating long day conditions (16 hours of illumination, 8 hours of darkness) due to the exhaustion of our plant resources. The memory time was 10 to 15 s shorter when *D. muscipula* was exposed to short day conditions (see Figure 5). We are tempted to regard this effect as an indirect one. Under short day conditions, the physiological conditions in general and photosynthetic productivity and energy supply in particular (Mayer & Hampp 1995) might be less favourable for the expression of the time memory. The importance may have been particularly enhanced since all time memory measurements were executed between 9 and 12 a.m., just after the beginning of the photoperiod at 8 a.m. This result is consistent with the interpretation that the closure movement of the *D. muscipula* trap, as in other nastic movements, is accompanied by a marked decline in ATP content in the tissues involved (Jaffe 1973; Williams & Bennett 1982; Fromm & Eschrich 1988). Meeting this energy demand might well be less problematic under continuous irradiation.

Effects from Seasonality and Leaf Age

We observed seasonal effects on the time memory of *D. muscipula.* In mid-May the time memory is clearly longer than in late June (see Figure 6). This difference includes all age classes of traps. For instance, in spring, relatively old traps exhibit a memory time of up to 75 s whereas in summer, traps of the same age show a time memory of just 50 s. Hence, the ontogenetic life cycle of the trap leaves of *D. muscipula*, which, of course, governs leaf emergence, leaf growth and leaf development, itself is subject of circannual variability (Roberts & Oosting 1958). This seasonality modulates the time memory of the Venus flytrap to a considerable extent.

The influence of the ontogenetic stage of the trap leaves on the time memory of *D. muscipula* was further confirmed by the effect of trap leaf age on the time memory. The younger the traps being investigated, the shorter was the time memory (see Figure 7). Time memory reached its maximum in the most fully developed traps; newly emerged trap leaves exhibited the shortest memory time. This result can be derived from the percentage of traps which responded to a fixed time interval (45 s) between first and second stimulation. The stimulation time interval for 50% closure shows exactly the same age effect. Evidently, mature leaves are superior to younger traps with respect to those anatomical and physiological conditions, which presumably are decisive for the manifestation of the time memory and its respective duration.

Stimulation Involving Different Trigger Hairs.

In addition to the external, i.e. environmental conditions, which have been tested above, a positional effect was also investigated, namely the stimulation of different trigger hairs and the influence thereof on the time memory. Indeed, the pattern of stimulation exerts a surprisingly strong influence on the time memory of *D. muscipula*. It makes a big difference whether the same trigger

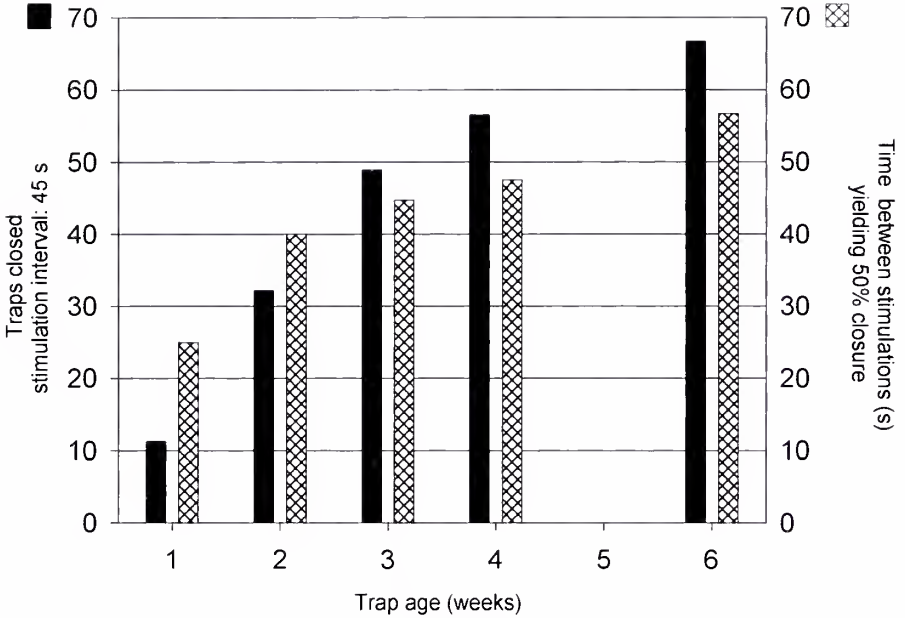


Figure 7: Influence of trap age on the time memory, expressed as the percentage of closures at 45 s time interval between stimulations (solid bars), or the number of seconds required to reach 50% closure values (crosshatched bars).

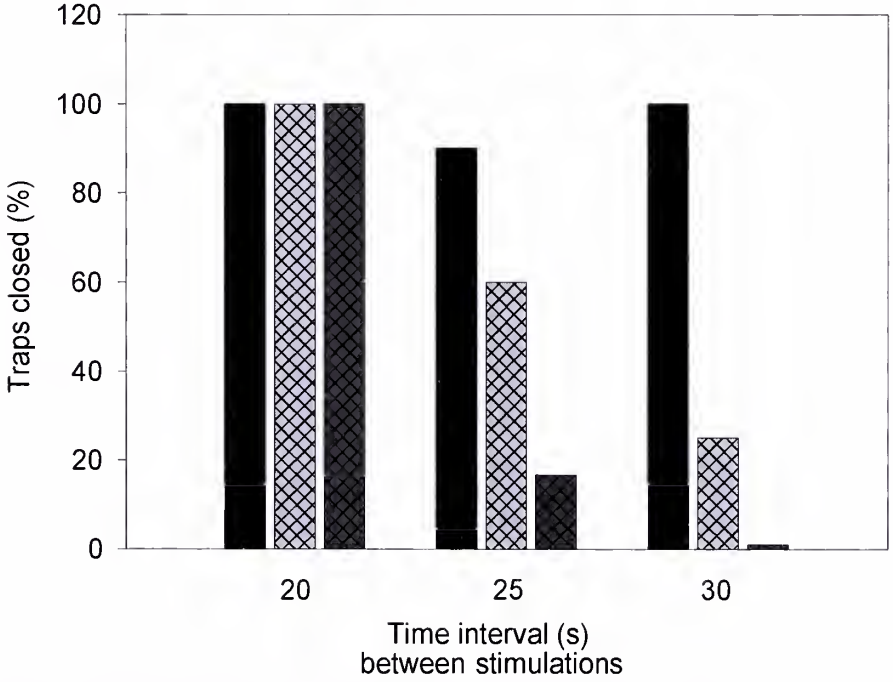


Figure 8: Position effect of the time memory. The second stimulation was executed either with the same trigger hair as before (shaded in black), or with an other hair, located either on the same lobe of the trap leaf (light grey), or on the opposite lobe (dark grey).

hair was successively stimulated twice, or two different hairs—located either on the same or on opposite lobes of the trap leaf—were stimulated one after the other. When a relatively short time-interval (20 s) between successive stimulations was applied, all traps closed, regardless of which hairs were touched or in which order (see Figure 8). However, when the interval between stimulations was extended to 25 s or even 30 s, the response of the traps depended very much on the mode of triggering. At 30 s, the percentage of traps that closed dropped almost to zero when two trigger-hairs on opposite lobes were stimulated successively. Stimulation of two different hairs, located on the same lobe also led to a decrease of memory time, but still about 20% closures were observed. An intermediate time interval, 25 s also caused a considerable and differential decrease in time memory, but the decline was less pronounced than at 30 s.

These results indicate a pronounced cooperativity of the sensitive hairs in triggering the closure movement. The differential response pattern of the time memory described above cannot be understood without assuming an exchange of information between the different trigger hairs of a trap leaf, the APs acting as the transmitter. Supposedly, the AP-signal of any first stimulation event is communicated to and perceived by all other sensitive hairs of the trap. This suggests that the time memory of *D. muscipula* cannot be attributed to any specific, exclusive cells/tissue loci, aside from the sensitive hairs, which exhibit a distinct AP-responsiveness. Fagerberg and Allain (1991) studied the dynamics of trap closure and reported that the movement is very much delocalized and all parts of the trap leaf are involved, although to differing extents. If, on the other hand, a distinct signal perception site really exists, it should not make a significant difference with respect to the resulting memory time, if the first and the second AP-signal is being perceived as a double signal from one and the same trigger hair, or if two different sensitive hairs are engaged in signal transduction.

Discussion

It has been demonstrated (see Figure 1) that while trap leaves that close incompletely apparently have a hampered closure mechanism, their time memories—although slightly shifted—are otherwise identical for total closures and all closures. This clearly shows that the time memory is not causally connected to the dynamics of the closure process. This closure-model predicts a state of mechanical bistability where both the open and the closed states are metastable to small perturbations. Assumedly, large, mature, and thus strongly curved leaves release more energy at this critical stage of movement and easily reach the state of complete closure. In contrast, smaller, more weakly curved, predominantly young leaves may get stuck before total closure is reached (Forterre *et al.* 2005).

The inverse temperature curve which characterizes the memory effect (see Figure 3) can be understood as the manifestation of a reaction (-series), which interacts antagonistically with the time memory, and which accelerates dramatically with rising temperature. If so, this reaction most likely governs the removal or redistribution of a compound, the intracellular level of which had been raised by the AP triggered by a first-stimulation event. The prime candidate for this compound in question is $[Ca^{2+}]_{cyt}$ (see Introduction). In this case, the antagonistic reaction could well comprise Ca^{2+} efflux from the cytosol, directed by Ca^{2+}-ATPases, located in the plasmalemma (and perhaps in the ER) of the cells which have been seized by the AP-wave. In fact, several ATPases have been found to exhibit extraordinarily high temperature coefficients (DeCoursey & Cherny 1998), exhibiting Q_{10}-values up to 5.3. This coincides quite well with a Q_{10} of about 4 for the decline of memory time between 20 and 30°C. In conclusion, the AP-induced enhanced level of $[Ca^{2+}]_{cyt}$ is supposed to decrease more rapidly at elevated temperatures due to a markedly enhanced activity of these Ca^{2+}-efflux pumps. As a consequence, much more rapidly $[Ca^{2+}]_{cyt}$ reaches a level, too low to be pushed beyond the critical threshold for closure by the subsequent second AP. However, the indicative value of the high Q_{10}, observed, must not be over-stressed since not only membrane transporters (DeCoursey & Cherny 1998; Zuñiga *et al.* 2004) but complex reaction sequences may exhibit above average temperature coefficients. The levelling-off of the temperature curve at >30°C and < 20°C indicate that functional integrity is rapidly lost even under not really extreme temperature conditions. In this respect, thermally induced membrane phase transitions, affecting transmembrane transport systems, e.g. the ATPases, supposedly involved in the time memory mechanism (see above), should be taken into consideration (Cooke & Burden 1990).

The interpretation of the strong position effect of stimulation (see Figure 8) is challenging and worth being discussed. If in fact the time memory is delocalized across the leaf blade of the traps,

as has been deduced above, then the propagating AP-signal, evoked by the stimulated trigger hair, assumedly starts the time memory clock everywhere across the leaf, but with a decreasing impact. Consequently, the more distant from the initially triggered hair the other hairs (stimulated thereafter) are, the weaker is the switch-on impact evoked at their respective site. For that reason, the first pulse must fade away more rapidly in the remote regions of the trap leaf than it does in the neighbourhood of the originally stimulated hair. It may be mentioned that this switch-on process does not necessarily consist of the initial rise in $[Ca^{2+}]_{cyt}$ itself (see Introduction). It could be a subsequent step in an intracellular signal chain, perhaps as a hypothetical regulator complex as hypothesized by Hodick & Sievers (1988). In any case, we find that within 30 s the second AP-pulse, evoked by a different (and remote) trigger hair, may be unable to drive the situation beyond the threshold requirement and thence trap closure. In case of a double-stimulation of the same trigger hair, after 30 s enough of the originally elevated $[Ca^{2+}]_{cyt}$ (or of any hypothetical factor) is still present to sustain the pre-closure condition of the trap. Two different trigger hairs, located next to each other, would represent an intermediate situation. The intermediate results obtained at 25 s time-lapse between stimulations support this interpretation.

The effects of irradiance (daily photon fluency), of seasonality and of trap leaf maturity (leaf age) on the time memory of *D. muscipula* are pronounced. While these results do not *per se* offer any clue for a deeper understanding of the mechanisms underlying time memory, they suggest that the time memory is deeply affected by a wide scope of physiological factors. Their variability within the natural ontogenetic band-width of trap leaves strongly radiates into the time memory mechanisms.

Conclusion

After about 130 years of observation, amazement, experimentation and interpretation, the Venus flytrap *D. muscipula* still deserves the attribute "this most remarkable of all plants" (Darwin 1875), and still, the plant is an enigma. One of the questions awaiting definite answers is the time memory. While the elucidation of calcium signalling and oscillations in $[Ca^{2+}]_{cyt}$ in guard cells and some other topics is far advanced on the methodological as well as on the theoretical scope (White 2000; Schroeder *et al.* 2001; Hetherington & Brownlee 2004), the corresponding aspects with regard to the time memory of *D. muscipula* have been completely neglected up to now. We were able to provide some new insights into the phenology of this intriguing phenomenon. They in turn may now hopefully revive and stimulate research on the molecular mechanisms of the time memory.

Acknowledgements: We are very much grateful to H. Zimmer and his team for expert nursing of the plants. This work was supported by E-Plus Mobilfunk GmbH und Co. KG (Düsseldorf, Germany) and Swisscom AG (Bern, Switzerland).

Literature Cited

Benolken, R.M., and Jacobson, S.L. 1970. Response properties of a sensory hair excised from Venus's-flytrap. J.Gen. Physiol. 56: 64-82.

Brown, W.H. 1916. The mechanism of movement on the duration of the effect of stimulation in the leaves of *Dionaea*. Amer. J. Bot. 3: 68-90.

Brown, W.H., and Sharp, L.W. 1910. The closing response in *Dionaea*. Bot. Gaz. 49: 290-302.

Burden-Sanderson, J. 1888. On the electromotive properties of the leaf of *Dionaea* in the excited and unexcited states. Phil. Trans. R. Soc. Lon. 179: 417-449.

Burden-Sanderson, J., and Page, F.J.M. 1876. On the mechanical effects and on the electrical disturbance consequent on excitation of the leaf of *Dionaea muscipula*. Proc. R. Soc. Lon. 25: 411-434.

Casser, M., Hodick, D., Buchen, B., and Sievers, A. 1985. Correlation of excitability and bipolar arrangement of endoplasmatic reticulum during the development of sensory cells in trigger hairs of *Dionaea muscipula* Ellis. Eur. J. Cell. Biol. 36 (Supp.). 12.

Cooke, D.T., and Burdon, R.S. 1990. Lipid modulation of plasma membrane-bound ATPases. Physiol. Plant. 78: 153-159.

Cosgrove, J.D., and Hedrich, R. 1991. Stretch-activated chloride, potassium and calcium channels coexisting in plasma membranes of guard cells of *Vicia faba* L. Planta. 186: 143-153.

Darwin, C. 1875. Insectivorous plants. Murray, London .
DeCoursey, T.E., and Cherny, V.V. 1998. Temperature dependence of voltage-gated H^+ Currents in human neutrophils, rat alveolar epithelial cells, and mammalian phagocytes. J. Gen. Physiol. 112: 503-522.
Fagerberg, W.R., and Allain, D. 1991. A quantitative study of tissue dynamics during closure in the traps of Venus's flytrap *Dionaea muscipula* Ellis. Am. J. Bot. 78: 647-657.
Forterre, Y., Skotheim, J.M., and Dumais, J., and Mahadevan, L. 2005. How the Venus flytrap snaps. Nature. 433: 421-425.
Fromm, J., and Eschrich, W. 1988. Transport processes in stimulated and non-stimulated leaves of *Mimosa pudica*. II. Energies and transmission of seismic stimulations. Trees. 2: 18-24.
Guttenberg, von H. 1925. Die Bewegungsmechanik des Laubblattes von *Dionaea muscipula* Ellis. Flora. 118: 165-183.
Guttenberg, von H. 1926. Die Bewegungsgewebe. In: K Linsbauer, ed, Handbuch der Pflanzenanatomie, Section 1, Part 2, Volume 5. Gebrüder Bornträger, Berlin pp 143-146.
Haberlandt, G. 1906. Sinnesorgane im Pflanzenreich. Zur Perzeption mechanischer Reize. 2 Ed. Engelmann, Leipzig: 133-143.
Harper, J.F. 2001. Dissecting calcium oscillators in plants. Trends Plant Sci. 6: 395-397.
Hetherington, A.M., and Brownlee, C. 2004. The generation of Ca^{2+} signals in plants. Ann. Rev. Plant Biol. 55: 401-427.
Hodick, D.M., and Sievers, A. 1986. The influence of Ca^{2+} on the action potential in mesophyll cells of *Dionaea muscipula* Ellis. Protoplasma. 133:83-84.
Hodick, D.M., and Sievers, A. 1988. The action potential of *Dionaea muscipula* Ellis. Planta. 174: 8-18.
Hodick, D.M., and Sievers, A. 1989. On the mechanism of trap closure of Venus flytrap (*Dionaea muscipula* Ellis). Planta. 179: 32-42 .
Jacobson, S.L. 1965. Receptor response in Venus's flytrap. J. Gen. Physiol. 49: 117-129.
Jaffe, M.J. 1973. The role of ATP in mechanically stimulated rapid closure of the Venus's-flytrap. Plant Physiol. 51: 1293-1302.
Juniper, B.E., Robins, R.J., and Joel, D.M. 1989. The carnivorous plants. Academic Press, London pp 46-129.
Malone, M. 1996. Rapid long-distance signal transmission in higher plants. Adv. Bot. Res. 22: 161-228.
Mayer, W.-E., and Hampp, R. 1995. Movement of pulvinated leaves. Progr. Bot. 56: 236-262.
Roberts, P.R., and Oosting, H.J. 1958. Responses of Venus fly trap (*Dionaea muscipula*) to factors involved in its endemism. Ecol. Monogr. 28: 193-218.
Schroeder, J.L., Allen, G.J., Hugouvieux, V., Kwak, J.M., and Waner, D. 2001. Guard cell signal transduction. Ann. Rev. Plant Physiol. Plant. Mol. Biol. 52: 627-658.
Sibaoka, T. 1966. Action potentials in plant organs. Symp. Soc. Exp. Biol. 20: 49-73 .
Sibaoka, T. 1991. Rapid plant movements triggered by action potentials. Bot. Mag. Tokyo. 104: 73-95.
Stuhlmann, O. 1948. A physical analysis of the opening and closing movements of the lobes of Venus's fly-trap. Bull. Torrey. Bot. Club. 75: 22-44.
Trebacz, K., and Busch, M.B., Hejnowicz Z., Sievers A. 1996. Cyclopiazonic acid disturbs the regulation of cytosolic calcium when repetitive action potentials are evoked in *Dionaea* traps. Planta. 198: 623-626.
Volkov, A.G., Shvetsova, T., and Markin, V.S. 2002. Waves of excitation and action potentials in Green Plants. J. Biophys. 82: 218a.
Wayne, R. 1994. The excitability of plant cells: With a special emphasis on *Characean* internodal cells. Bot.Rev. 60: 265-367.
White, P.J. 2000. Calcium channels in higher plants. Ann. Bot. 81: 173-183.
Williams, S.E. 1973. The memory of the Venus' flytrap. Carniv. Pl. Newslett. 2: 23-25.
Williams, S.E., and Bennett, A.B. 1982. Leaf closure in the Venus flytrap: An acid growth response. Science. 218: 1120-1122.
Williams, S.E., and Mozingo, H.N. 1971. The fine structure of the trigger hair in Venus's flytrap. Amer. J. Bot. 58: 532-539.
Williams, S.E., and Pickard, B.G. 1980. The role of action potentials in the control of capture movements of *Drosera* and *Dionaea*. In: F. Skoog ed., Plant growth substances. Springer, Berlin, Heidelberg, New York pp 470-480.

Insecticidal Characteristics of the Desert Stingbush *Eucnide urens*

Michael Metzler • 658 N. Ranch Wood Trail • Orange, CA 92869 • USA • michael_metzler@yahoo.com

Keywords: ecology: animal interactions, *Eucnide urens* – observations: California (USA), *Eucnide urens*.

Death Valley is a famous desert area of the southern borderlands of California and Nevada, in southwestern USA. In 2004-2005, the winter storms brought record rainfalls to Death Valley, and the following spring saw a spectacular show of color to the landscape. The normally forbidding landscape was brought to life with primroses, larkspurs, poppies, verbenas, lilacs, phacelias, and a vast array of flowers in the daisy family. With the abundance of food provided by these flowering plants came a boost in the Valley's insect population. However, during this season my wife and I observed a surprising insect-plant relationship; one that was certainly not of benefit to the desert insects!

In April 2005, we toured Death Valley and were captivated by the fields of golden blooms separating the white salt flats on the valley floor and the black basalt mountains that rose in the distance. Driving west on Highway 190 we headed for the small village of Stovepipe Wells, where we turned onto a dirt road for a 5 km (3 mile) jaunt to Mosaic Canyon. As we were driving up the washboard road rising up from the valley, my wife mumbled something between the bumps about bringing an iron bra next time. We parked at the wide bahada where water fans out as it exits the mouth of the canyon.

Figure 1: Young and old foliage. Note the insects are retained on the dead foliage.

Figure 2: Close view of *Scaeva pyrastri* attached to the armed flower peduncle.

Figure 3: A large flowering plant.

As we hiked up the canyon, the walls became gradually narrower and the name for Mosaic Canyon became apparent. The destructive damage of water over the millennia have carved through the sediment, exposing the layers agglomerated fragments of marble giving the appearance of an ancient Roman bath. As we continued our trek, the walls of the erosive path progressed to solid marble which had been highly polished. The canyon was almost devoid of plants except for those that could manage to survive growing out small crevices in the canyon wall.

One of these durable plants, bearing powdery white flowers, drew my attention—it was almost entirely covered in insects! Upon closer examination, the insects appeared to be all hoverflies (*Scaeva pyrastri*). They seemed to be stuck flat to the stems and undersides of the leaves. The undersides of some leaves were completely covered in insects! No insects were adhering to the tops of these leaves.

The undersides of the leaves had the texture of sandpaper because they were covered with fine, rough bumps. Numerous white trichomes (hairs) on the upper leaf surface inflicted painful stings when touched, similar to stinging nettles (*Urtica dioica*). There were no tacky or adhesive substances on the leaves, so it was not readily apparent why the insects were becoming stuck to the plant so quickly. I decided to watch a plant carefully. I saw that when a hoverfly landed on the top side of a leaf, it quickly walked to the underside, where it stopped close to the leaf margin. It struggled, then it stopped moving! Prodding the fly produced no movement of any part, including from the wings which were not in contact with the leaf.

Interestingly, hoverflies appeared to be in unusually high number in the canyon. I do not know if they are normally found in high numbers in the canyon or if they are lured there by some attractive property of the plant. I saw hoverflies in the plant's flowers, possibly lured by the pollen. Do the leaves produce an attractive property as well?

Upon returning from Death Valley, Barry Rice and Jan Schlauer from The International Carnivorous Plant Society identified the plant as a desert rock-nettle or stingbush (*Eucnide urens*, in the Loasaceae family). The name of this plant adequately describes the effect of specialized trichomes on the top of the leaves. However, a literature search did not reveal any information on the insecticidal characteristics of the desert stingbush. Eisner *et al.* (1998) describes a similar characteristic of the *Mentzelia pumila* (desert blazing star), also in the Loasaceae family. Another name for this plant is stickleaf, for its ability to stick to clothing like Velcro®. Eisner *et al.* (1998) studied the insect entrapping abilities of *Mentzelia pumila* extensively. Electron microscopy revealed several types of specialized trichomes with curved barbs which act as grappling hooks to immobilize the insects. Other trichomes may act to puncture the insect. There was no description of the nettle-like trichomes found on *Eucnide urens*. The insect-trapping trichomes of *Mentzelia pumila* are not restricted to the underside of the leaf and stems.

The evolutionary benefits of these hooked trichomes are not readily apparent. One possible benefit is that the insects may be providing a nutritional benefit to the plant. It may be that the plant can absorb moisture or other nutrients from direct contact with the insect. Another possible benefit may be that when the insect-littered leaves fall to the ground and decay, they may provide nutrients that are lacking in the soil.

References:

Eisner, T., Eisner, M., and Hoebeke, R.E. 1998. When defense backfires: Detrimental effect of a plant's protective trichomes on an insect beneficial to the plant. Proc. Natl. Acad. Sci. 95: 4410-4414.

Looking Back: CPN 25 years ago

Bruce Lee Bednar published a contrite and candid confession about the first time he ever saw pitcher plants (*Sarracenia* and *Drosera*) in the wild, sixteen years earlier (1965) in the New Jersey Pine Barrens: "One tends to get frenzied, almost hysterical, with a first encounter with carnivorous plants in the wild. Conservation was the last thing on this young person's mind. Not taking time to think (at all), I pulled up every *purpurea* I could find. To make matters even worse, I returned that fall with a friend and removed the last four plants we found. Certainly very poor judgement on my part." Bruce mentioned he visited the site years later "out of guilt" and was relieved to see that plants were still present, possibly having resprouted from broken rhizomes. This editor (BR), a diehard conservationist, can sympathise having committed similar youthful sins. It is an ICPS conservation goal to transform collector interest from poaching pressures that harm carnivorous plants, into legal activities that aid wild populations.

Additional notes on *Eucnide urens* (Parry ex Gray) Parry in the Family Loasaceae

Barry Rice • P.O. Box 72741 • Davis, CA 95617 • USA • barry@carnivorousplants.org

Keywords: ecology: *Eucnide urens, Menzelia pumila.*

Michael Metzler (2006) gave such an interesting account of *Eucnide urens* that it is worth providing additional information about the plant. *Eucnide urens* is in the Loasaceae family, a group of about 15 genera and 260 species in the Americas, Africa, and the Middle East. Plants in this family (which includes herbs, shrubs, and small trees) often are covered with stiff hairs that may be stinging, grappling, or gland-tipped (Mabberley 1997). For an excellent set of photographs of these remarkable trichomes (hairs) on *Menzelia pumila* (also a member of the Loasaceae), refer to Eisner *et al.* (1998). In that paper, three types of trichomes are described and called type 1, 2, and 3. Type 1 trichomes are tall and slender, with a rosette of recurved barbs making the trichomes exactly like a grappling hook. Type 2 trichomes are larger, conical, and with a pointed tip. Type 3 trichomes are intermediate in size, conical, but with a grappling-type of tip. The grappling hooks function to retain insects, the others cause mechanical damage to them. Studying herbarium specimens of *Menzelia pumila*, I observed that the upper leaf surfaces had only type 2 trichomes, the lower leaf surfaces had mostly type 1 trichomes and occasional type 2 trichomes, while the leaf margins had type 3 trichomes.

The genus *Eucnide* comprises fourteen species (Mabberley 1997), including the Texan species *E. bartonioides* Zucc. which while stinging, is sometimes cultivated. The genus includes annuals, biennials, and perennials that range from small herbs to sub-shrubs. *Eucnide urens* occurs in the desert provinces of California, Nevada, Utah, Arizona, and northern Mexico, especially in creosote (*Larrea tridentata*) bush scrub communities at elevations below 1400 m (4600 feet) (Hickman *et al.* 1993).

I viewed the leaf surfaces of *Eucnide urens* from Death Valley (Titus Canyon, DAV #151283) at 30-100 X, and verified that *Eucnide urens* has trichomes. The upper leaf surfaces bear unbarbed stinging spines 4-5 mm long. The lower surfaces bear type 1 grappling trichomes 0.6-1.5 mm long and occasional stinging spines. The stems, peduncle, and calyx lobes are especially densely armed with spines and type 1 trichomes up to 2 mm long. Type 2 and type 3 trichomes are absent on *Eucnide urens*[1]. What makes *Eucnide urens* so particularly unpleasant to insects is the addition of the long stinging spines, as they can inject venom. Apparently, the venom that *Eucnide* injects is toxic to *Scaeva pyrastri*. While Metzler (2006) notes that insects on *Eucnide* died almost instantly, Eisner *et al.* (1998) reported that in the case of insects on *Menzelia pumila*, "death came slowly to those caught, and that survival was still an option for those able to pull loose."

The value of trapping insects to *Eucnide urens* is mysterious. A review of images on the internet and of herbarium specimens of *Eucnide urens* at UC Davis (DAV) revealed no other recorded incidences of large numbers of insects captured on the plant surfaces. While it might be attractive to suggest the possibility of some sort of insect carnivory, or soil-enhancement by the carcasses of dead prey—such as theorized by Eisner *et al.* (1998) in the case of *Mentzelia pumila*—trapping insects does not seem to be a consistent activity by *Eucnide urens*. The observations by Metzler (2006) seem to be of a serendipitous event. However, it certainly is enjoyable

[1]The stinging spines of *Eucnide urens* are probably analogous to the type 2 trichomes of *Menzelia pumila* because their distributions on their respective plants are the same. Also, the stinging spines are set atop venom glands, and similar structures can be seen at the base of the type 2 trichomes.

speculating how such accidental innovative activities could, in the past, have encouraged the development of carnivory in modern carnivorous plants. Perhaps if left to evolve for many millennia, plants such as *Eucnide urens* might develop into novel carnivorous species!

Why were the hoverflies attracted to the *Eucnide urens* plants in such large numbers? As an adult, *Scaeva pyrastri* feeds on nectar and pollen (Bugg 2006, pers. comm.), and in fact is apparently quite selective in the flowers it feeds upon (Bugg 1992; Colley & Luna 2000). As its common name implies, hoverflies are skilled aerialists and are not weakly-flying insects that blunder into surfaces accidentally. The *Scaeva pyrastri* in Death Valley were obviously drawn to the plant. Were they attracted to the flowers as the only available source of food in Mosaic Canyon, and landed on the leaves only to rest?

Another possibility is that the insects were interested in the plant as a site to lay eggs. While as an adult *Scaeva pyrastri* is a flower feeder, its larvae are voracious feeders on aphids—a single *Scaeva pyrastri* larva may consume 500 aphids in its development (Bugg 1992)[1]! Is it possible that the hoverflies were attracted to the plants because of an aphid infestation? Metzler (2006) did not mention seeing large numbers of aphids present, nor are they visible on his photographs. There are droplets of brown fluid staining the rock surface under the plants—it is unclear whether these are from hemolymph (blood) from the trapped insects, sugary exudates from a hidden aphid population, or exudates from the plant?

Clearly, this is something new for observant "flower-peepers" to look for in their annual spring treks through the deserts of the USA!

References:

Bugg, R.L. 1992. Habitat manipulation to enhance the effectiveness of aphidophagous hover flies (Diptera: Syrphidae). Sustainable Agriculture Technical Reviews. 5(2).

Colley, M.R., and Luna, J.M. 2000. Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). Environmental Entomology 29(5): 1054-1059.

Eisner, T., Eisner, M., and Hoebeke, R.E. 1998. When defense backfires: Detrimental effect of a plant's protective trichomes on an insect beneficial to the plant. Proc. Natl. Acad. Sci. 95: 4410—4414.

Hickman, J.C. (editor) 1993. The Jepson Manual: Higher plants of California. University of California Press. Berkeley. 1402p.

Mabberley, D.J. 1997. The Plant-Book (2nd ed.). Cambridge University Press. Cambridge. 858p.

Metzler, M. 2006. Insecticidal characteristics of the desert stingbush *Eucnide urens*. Carniv. Pl. Newslett. 35: 119-121.

[1]Many of the trapped insects that Eisner *et al.* (1998) observed on *Mentzelia pumila* were a species of Coccinellid beetle, *Hippodamia convergens*, that preys upon aphids. Astonishingly, despite its extensive trichome defenses, *Mentzelia pumila* is attacked by an aphid (*Macrosiphum mentzeliae*) that manages to roam the plant in safety—protected from predators by the very trichomes that should function to protect the plant!

Carnivorous Plant Specialist

Visit us at www.plantsforkids.com

Live delivery guaranteed.
Gift packages & fundraising kits

CITES No. US839095

Barry Rice (barry@carnivorousplants.org) writes: This autumn I had the pleasure of touring a few *Sarracenia purpurea* sites managed by the Massachusetts office of The Nature Conservancy, including a calcareous fen. I was surprised to discover that Hawley Bog—a *Sphagnum* bog site well known to New England carnivorous plant enthusiasts—had plants that were extremely pale with only a tiny bit of venation. The day after I saw these plants, I saw somewhat similar specimens at a Vermont bog that can only be accessed after a few hours of hiking and bushwacking deep in the Green Mountain National Forest. These Massachusetts and Vermont plants are very similar to the "semi-veinless" plants that Mazur & Lechtman reported upon in CPN (2005; 34:3, p79-84), especially the plants in their figure 5 and the foreground of figure 7. I had the pleasure of visiting Mazur & Lechtman's Canadian study sites, and agree that the "veinless" and semi-veinless plants in their study seem to have arisen from the hybridization of normally pigmented plants with anthocyanin-free *S. purpurea* f. *heterophylla* (which in the USA is only reported in Michigan, New York, and New Jersey). The presence of semi-veinless plants in Massachusetts and Vermont suggests that the rare *S. purpurea* f. *heterophylla* might have occurred in in these states in the past. (The Massachusetts sites are under intensive study, and so it is unlikely that the plants might occur there today and not be noticed.) Visitors to Hawley Bog must stay on the boardwalk, but fortunately fine examples of the semi-veinless plants grow right next to the path and so can be closely observed without damaging the fragile bog mat. I will be posting a trip report on my web site (www.sarracenia.com) in a few months, and will present images of these interesting plants.

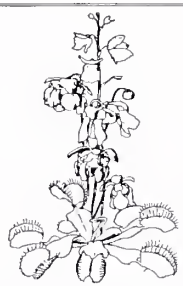
Barry Rice (barry@ carnivorousplants.org) writes: I have just learned that staff of The Nature Conservancy and dedicated volunteers spent 8 October digging *Sarracenia alata* plants from a strip of land that is being developed for housing north of New Orleans, in St. Tammany Parish. ("Parish" is a Louisiana designation for an area of land, similar to "county"—Louisiana must, of course do things differently!) The population in this parish has grown a great deal after Hurrican Katrina, and bulldozers are busy making room for all the new people. The 2000 plants will be cared for over the winter, until they can be replanted in less threatened sites. The Louisiana chapter of The Nature Conservancy received a $2000 grant from the ICPS Conservation Program in 2006 to support this kind of work. Good job!

Have you donated to the ICPS this year?

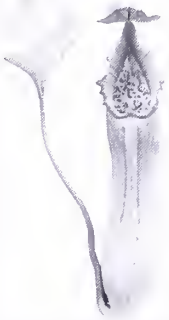
Don't forget that the ICPS is a 501(c)3 nonprofit organization, and donations to it are tax deductible (as least for members in the USA). Send your donation to the ICPS before the end of the calendar year! Help support our conservation and educational programs!

Nursery & *Garden*
NATURE ET PAYSAGES

32360 Peyrusse-Massas FRANCE
Price List free, more than 400 varieties
e-mail: nature-et-paysages@mipnet.com
FAX: 00-33-(0)-5-62-65-50-44



New in 2006, shop online at http://www.natureetpaysages.fr



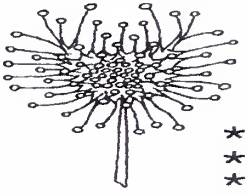
CASCADE CARNIVORES

Carnivorous Plant Nursery

- ***Drosophyllum lusitanicum***
  - *Yes, we ship Dewy Pine plants - live delivery guarantee*
- ***Nepenthes***
  - *highland species are our specialty*
- ***Drosera, Pinguicula, Utricularia, Byblis, Heliamphora, VFTs** and more*

Visit us on the web - http://www.cascadecarnivores.com
email - support@cascadecarnivores.com

When in Northern California Visit



California Carnivores

Specializing in insect-eating and other exotic plants

* Open all year, call ahead in winter
* Commercially cultivated
* Over 500 varieties on display
* On site & domestic mail order
* We ship potted plants

2833 Old Gravenstein Hwy South, Sebastopol, CA 95472
(707) 824-0433 **Price List – SASE**
Visit us on the Internet at http://californiacarnivores.com

TRIFFID PARK

257 PERRY ROAD, KEYSBOROUGH, VIC, 3173, AUSTRALIA
PHONE: 61 (0)3 9769 1663, 11am to 5pm Monday to Thursday ONLY
FAX: 61 (0)3 9769 1663, 8am to 8pm, 7 days per week
EMAIL: triffids@triffidpark.com.au WEB: www.triffidpark.com.au
Owned and operated by Colin and Tina Clayton. Managed by Donna ClaytonSmith.

FOR ALL YOUR **CARNIVOROUS PLANT** REQUIREMENTS INCLUDING:
PLANTS, POTS, LABELS, BOOKS, SEEDS, SPHAGNUM MOSS AND PEAT MOSS
WRITE, PHONE, FAX OR EMAIL TRIFFID PARK FOR A FREE COLOR
MAIL ORDER CATALOGUE OR VIEW OUR COMPREHENSIVE WEB SITE.

You are most welcome to visit Triffid Park but please organise this with us first,
as inspection is by appointment **ONLY**.

Carolina Carnivorous Gardens

"Specializing in insect eating plants"

★on site sales & display gardens
★call ahead for appointment
★U.N.C.C. *Sarracenia* hybrids
★winter hardy *Drosera* species
★plants commercially propagated

1509 Little Rock Road Charlotte, NC 28214
Phone: 704-399-3045 Cell: 704-458-8538
http://personal.atl.bellsouth.net/clt/f/l/flytrap1/index.html
Contact: DAVID CRUMP Price list - S.A.S.E.

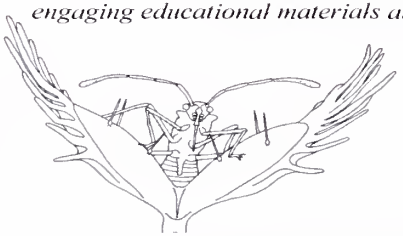
Cook's Carnivorous Plants

P.O. Box 2594 Eugene, Oregon 97402
541/688-9426
http://www.flytraps.com/

Specializing in the strange and unusual plants since 1992
Over 150 varieties available for purchase at all times, as well as live moss and your needed supplies
By appointment on site sales.....Shipping year round worldwide!!
Give us a call from 9Am to 6Pm Pacific Coast time Monday thru Friday check us out on the web anytime
Email support through cooks@flytraps.com

Carnivorous Plant Nursery

Promoting environmental stewardship through engaging educational materials and low-cost, high-quality carnivorous plants.



- Carnivorous Plants
- Bog Orchids, Bog Plants
- Activity Book for Carnivorous Plants
- Bugs in the Bog Board Game
- Free Monthly Drawing
- OnLine Shopping and Mail Order

16128 Deer Lake Road, Derwood, MD 20855
http://www.carnivorousplantnursery.com
Phone: 301-519-7505 Email: info@carnivorousplantnursery.com

Index of Contributors

Adamec, Lubomír ---- 19,52
Adlassnig, W. ---- 84
Benes, Karel ---- 19
Brittnacher, John ---- 3,35,67,99
Clemens, William Joseph ---- 12,32
Cokendolpher, James C. ---- 23
Conner, David ---- 79
DePuy, Gary ---- 91
Gastinel, Louis ---- 52
Gibson, Robert ---- 39,64,65,70
Gibson, Thomas C. ---- 88
Hind, Chris ---- 69
Kohout, Pavel ---- 19
Kováãik, Josef ---- 49
Lechtman, Jay ---- 68,96
Lampard, Stan ---- 4
Lichtscheidl, I.K. ---- 84
Locke, Stephen ---- 100
Luhrs, Hans ---- 4
Metzler, Michael ---- 119,128
Molis, Arne ---- 108
Nerz, Joachim ---- 43
Patten, Gabriele ---- 108
Peroutka, M. ---- 84
Peruzzi, Lorenzo ---- 89
Pois, W. ---- 84
Repãák, Miroslav ---- 49
Rice, Barry ---- 31,34,57,88,92,93,122,124
Rivadavia, Fernando ---- 56
Rondeau, J. Hawkeye ---- 76
Schlauer, Jan ---- 10,31,52,57
Selwyn, Aidan ---- 97,100
Skau, Ken ---- 74
Snyder, Ivan ---- 68
Studnicka, Miloslav ---- 59
Teichreb, Chris ---- 36
Vieira, Sebastian ---- 1,14
Weidner, Manfred ---- 108
Wistuba, Andreas ---- 43
Wyman, Travis H. ---- 14

Referees/Correspondents:

The editors of Carnivorous Plant Newsletter and the officers of the International Carnivorous Plant Newsletter thank the following authorities for acting as external referees for the papers requiring anonymous peer review in 2006: L. Adamec, K. Baumgartner, S.J. Casper, C. Clarke, E. Dean, O. Gluch, J. Lechtman, L. Legendre, R. Mues, F. Rivadavia, E. Schlosser, D. Spencer, M. Studnicka, A. Stemler, O. Votrubova, and others.

Special Correspondents for the ICPS are: S.J. Casper (Germany), R. Gibson (Australia), M.K. Janarthanam (India), K. Kondo (Japan), F. Rivadavia (Brazil), S. Zamudio (Mexico).